COAST LIVE OAK (*QUERCUS AGRIFOLIA*) EFFECTS ON GRASSLAND BIOMASS AND DIVERSITY

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ABSTRACT

Spatial variation in environmental conditions and herbaceous community structure was studied across the ecotone between coast live oak (*Quercus agrifolia*) woodland and grassland in northern California. Oak canopy reduced light incidence (2.8% compared to open) but increased soil moisture and nitrogen availability underneath. The understory herbaceous layer had a different species composition from open grassland, lower species richness, lower above-ground biomass, a delayed seasonal growth, and different biomass partitioning by species. Grassland diversity and biomass fitted a second order polynomial regression, with maximum at 570 gm^{-2}, and reduced diversity in the harsh, shaded, low-productivity understory. The heterogeneity of physical conditions induced by oak canopy maintains a higher landscape (gamma) diversity of herbaceous plants.

Coast live oak (*Quercus agrifolia*) woodlands extend along the coastal hills and plains of California, from San Diego to Mendocino County, covering about 3350 km^2 (Griffin and Critchfield 1972; Bolsinger 1988). The oak woodland intersperses frequently with open grassland, forming a landscape mosaic.

The dominant evergreen coast live oak trees change environmental conditions in the understory, in terms of reduced light, less extreme temperatures, altered water availability and evapotranspiration, and soil enriched in nutrients and organic matter (Parker and Muller 1982). Grassland species composition and production consequently differ considerably under canopy compared to open.

We have previously reported differences in soil seed bank and seedling establishment patterns between open grassland and coast live oak understory in northern California (Marañón and Bartolome 1989). In this paper we document community-level grassland changes along the ecotone between coast live oak (*Quercus agrifolia*) woodland and open grassland, in the same study area. Features of the community structure studied were species composition, above-ground biomass and its seasonal partitioning among species, and species richness. We show how tree canopy influences plant diversity

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in this evergreen oak-dominated landscape. Small-scale changes in understory diversity should be important for maintaining biological diversity in managed landscapes.

Methods

Study site. The study was located at the University of California's Russell Reservation, about 20 km inland from San Francisco Bay, in the Coast Range. The climate is of mediterranean-type, with cool, humid winters and warm, dry summers. Annual precipitation averaged 1080 mm in 1982–1983, and 520 mm in 1983–1984, whereas the average annual rainfall (14 years) was 680 mm. Mean annual temperature was 14°C with a maximum monthly mean of 28°C in July and a minimum monthly mean of 5°C in December.

Sandstone hills are overlaid by a loamy, inceptisol (Millsholm series) soil. A South-facing 20° slope covered by annual grassland and bounded on East and West by coast live oak (*Quercus agrifolia*) woodland was selected as the study area. The oak canopy cover was over 90% with average density of 170 trees ha^{-1} and average dbh of 46 cm. On the reservation, no grazing by livestock has been allowed for the last 20 years, but impact by deer, voles and gophers may be locally important (Marañón and Bartolome 1989).

Sampling. Four transects were located across the oak woodland–open grassland ecotone, two on the east and two on the west boundaries of a grassland. Five 1 × 1 m plots were located along each transect, one representing the oak understory (1–3 m from the trunk and more than 7 m inside from the oak canopy edge), one in the open grassland (more than 5 m outside from the canopy edge) and three at the canopy edge (where more spatial variation is expected). In each plot, a square of 25 × 25 cm was located randomly and the aboveground biomass inside was clipped. The operation was repeated (excluding previous clipping sites) eight times during the growing season 1983–1984. The clipped biomass was sorted by species, oven-dried at 65°C and weighed.

Ten plots of 25 × 25 cm were randomly located in each of three defined habitats: oak understory, oak canopy edge and open grassland. Aboveground biomass was clipped on May 1983, separated into dead (mulch) and live plant materials, oven-dried at least 24 hours at 65°C and weighed.

Environmental conditions. Light incidence at the herbaceous level was measured at noon in July (five measurements on each plot), using a LI-COR Quantum Sensor.

Soil moisture was measured using the gravimetric method. The weight loss of 10 cm depth soil cores was recorded after 24 hours

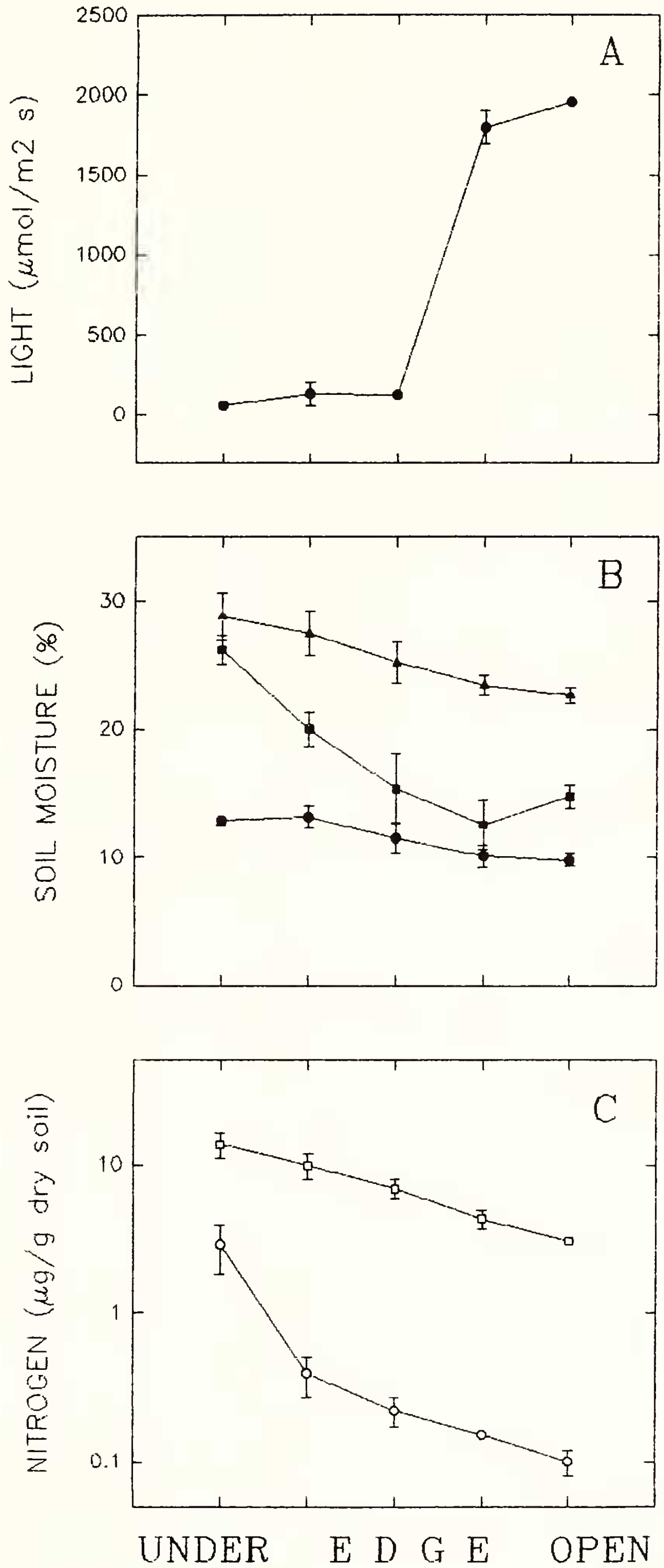

FIG. 1. Environmental variables along the ecotone between oak understory and open grassland (mean and standard error bar). A: Light incidence at noon July 30 (n = 15); B: Soil moisture (n = 4) in October 18 (●), December 12 (▲) and March 30 (■); C: Nitrogen content in top soil (n = 4), as nitrate (○) and ammonium (□).

oven-drying at 105°C. Soil moisture measurements were made in October and December 1983, and in March 1984.

Inorganic nitrogen, as nitrate and ammonium, in top soil samples from March 1984 was determined in KCl extracts colorimetrically (Jackson et al. 1988).

Numerical analysis. Species composition and abundance of twenty (5 plots from 4 transects) aboveground biomass samples from May 1984 were analyzed with detrended correspondence analysis (DCA) using a CANOCO program and selecting the following options: detrending by 2nd order polynomial, logarithmic transformation of the biomass data, exclusion of infrequent species (F = 1), and downweighting of rare species (Ter Braak 1988).

Grassland peak aboveground biomass and species richness, as well as environmental variables were averaged among the four transects to obtain a general spatial trend along the oak understory-open grassland ecotone. Cumulative species richness along the transect was calculated to reflect landscape (gamma) diversity.

The relationship between peak aboveground biomass and species richness was studied using both the 30 random samples from 1983 and the 20 plot samples from 1984 (total of 50 samples). A second order polynomial regression was fitted and the biomass for maximum diversity (BMD) was calculated as the curve's maximum (García et al. 1993).

Species nomenclature follows Munz (1968).

Results

Environmental conditions. July mid-day light incidence at the herbaceous level under the evergreen oak canopy averaged 53.8 μmol m^{-2} sec^{-1}, although sunfleck measurements reached 139 μmol m^{-2} sec^{-1}. At the oak canopy edge the average incident radiation increased to 125–130 μmol m^{-2} sec^{-1} and just outside the canopy projection the light sharply increased to 1794.7 μmol m^{-2} sec^{-1} (about 14 times) in the zone with shading during early and late daytime period. The average full sun radiation recorded in open grassland was 1950.7 μmol m^{-2} sec^{-1} (Fig. 1A).

Soil moisture at the beginning of the rainy season (October 18) was relatively low (9.8–12.9%) along the transect. Two months later (December 12) the top soil was moist (22.7–28.8%) all along the transect. On both dates, the oak understory soil was slightly moister than open grassland soil. Major changes of top soil moisture were observed during early spring (March 30), at the time of rapid plant growth, when open grassland soil suffered a more rapid water loss than understory soil (Fig. 1B).

Nitrogen content of the top soil, either as nitrate or ammonium,

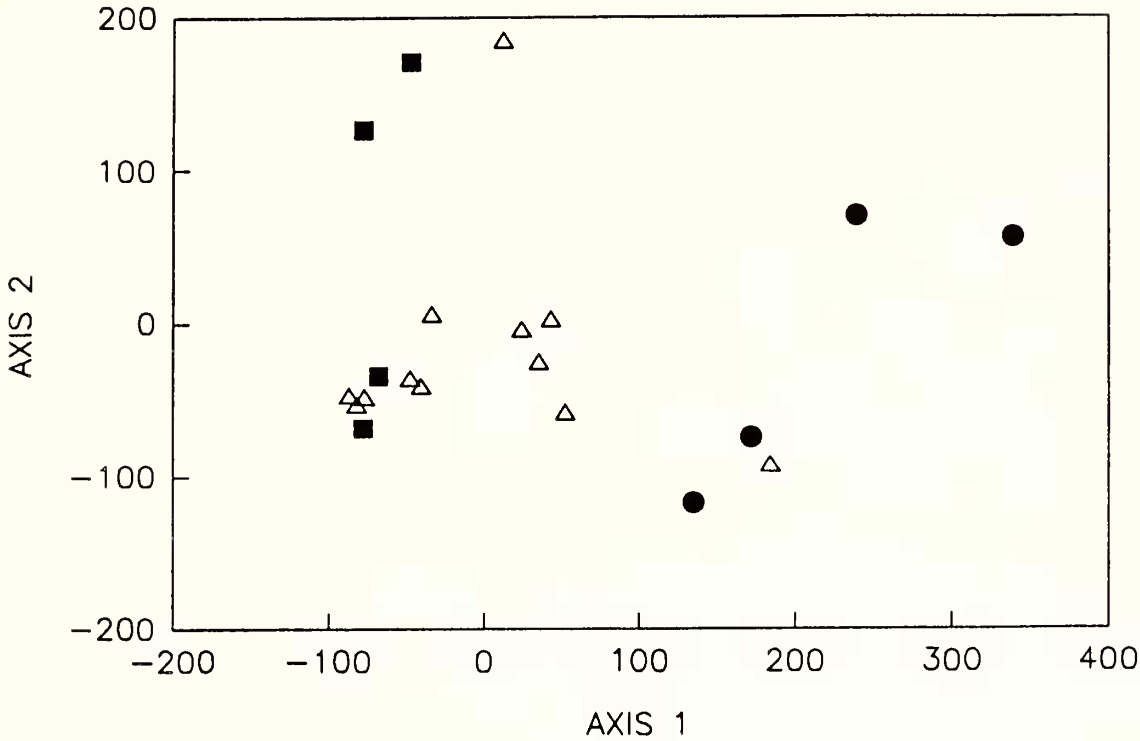

FIG. 2. DCA analysis of aboveground biomass samples from the oak understory (●), canopy edge (△) and open grassland (■).

showed a decrease along the transect, from the oak understory towards the open grassland (Fig. 1C). Mean nitrate content, in March, near the oak trunk was 2.9 $\mu g\ g^{-1}$ dry soil, decreasing at the oak canopy edge (0.15–0.39 $\mu g\ g^{-1}$ dry soil) and the minimum value was recorded in the open grassland soil (0.10 $\mu g\ g^{-1}$ dry soil). Ammonium content in top soil decreased more slowly from the inner oak understory (13.62 $\mu g\ g^{-1}$ dry soil) towards the oak canopy edge (4.32–9.86 $\mu g\ g^{-1}$ dry soil), and the minimum value was in the open grassland soil (3.07 $\mu g\ g^{-1}$ dry soil).

Species composition. DCA analysis of 26 species biomass in 20 samples clearly separated oak understory samples (at the right extreme of axis 1) from open grassland samples (at the left extreme of axis 1), whereas canopy edge samples are dispersed in-between and tend to be closer to the open grassland samples (Fig. 2). *Stellaria media, Galium aparine, Montia perfoliata* and *Carduus pycnocephalus* are among the species with higher positive scores for axis 1, differentiating the oak understory samples. *Bromus mollis, Geranium dissectum, Vicia sativa* and *Lupinus bicolor* show high negative scores for axis 1, and they are characteristic of open grassland samples.

Peak aboveground biomass. The average aboveground biomass in the oak understory, near the tree trunk (128.9 $g\ m^{-2}$) increased almost three times at the canopy edge (359.8 g m^{-2}), with a similar value to the open grassland (365.7 g m^{-2}) (Fig. 3A).

Seasonal biomass. The fastest increase of biomass in the open grassland occurred between February and April, and by June most of the plants were dried up. In the oak understory, the growth was slower than in the open but the decline was retarded, some plants remaining green until July (Fig. 4). The canopy edge samples showed a similar growth pattern to the open grassland samples but the decline at the end of the cycle was delayed, e.g., June aboveground biomass accounted for 90.8 g m^{-2} at the oak canopy edge and 12.1 g m^{-2} in the open.

Biomass partitioning by species. In the oak understory, *Montia perfoliata, Stellaria media* and *Galium aparine* made up 56% of the aboveground biomass early in the growing season (February), declining as a proportion of the community biomass in spring. *Carduus pycnocephalus,* with slower growth, was the dominant species later in the growing season, and some plants survived until July. *Bromus diandrus* and *Lolium multiflorum* were the most abundant annual grasses throughout the growing season. No annual legumes were recorded in the transect understory samples (Fig. 5A), although the perennial *Lathyrus vestitus* was present in a few (30%) of the random samples.

Typical understory species like *Montia perfoliata, Stellaria media* and *Galium aparine* only summed up to 3.8% of the aboveground biomass at the oak canopy edge. *Carduus pycnocephalus* (9%) and *Bromus diandrus* (12.2%) showed a significant biomass contribution in May samples. *Lolium multiflorum* was the dominant species (49.6%) in the spring community biomass. Other annual grasses, like *Bromus mollis* and *Avena fatua,* as well as annual legumes like *Medicago polymorpha* and *Vicia sativa* had a minor biomass contribution. Perennial *Elymus triticoides* and *Aster chilensis* increased their biomass proportion later in the growing season (Fig. 5B).

Four annual grasses, *Bromus diandrus, Lolium multiflorum, Avena fatua* and *Bromus mollis* made up 88.1% of the spring aboveground biomass in the open grassland. *Carduus pycnocephalus* represented 12.9% of the biomass in the April samples. A few annual legumes, *Lupinus bicolor, Vicia sativa* and *Medicago polymorpha* summed up to 14.5% of the community biomass in May. Other important species, in term of biomass, were *Hypochoeris glabra, Geranium dissectum* and later in the growing season, the perennial *Elymus triticoides* (the only living biomass in July samples) (Fig. 5C).

Species richness. Species density was lower near the oak trunk (average of 5.8 species 0.0625 m^{-2}) than at the oak canopy edge or

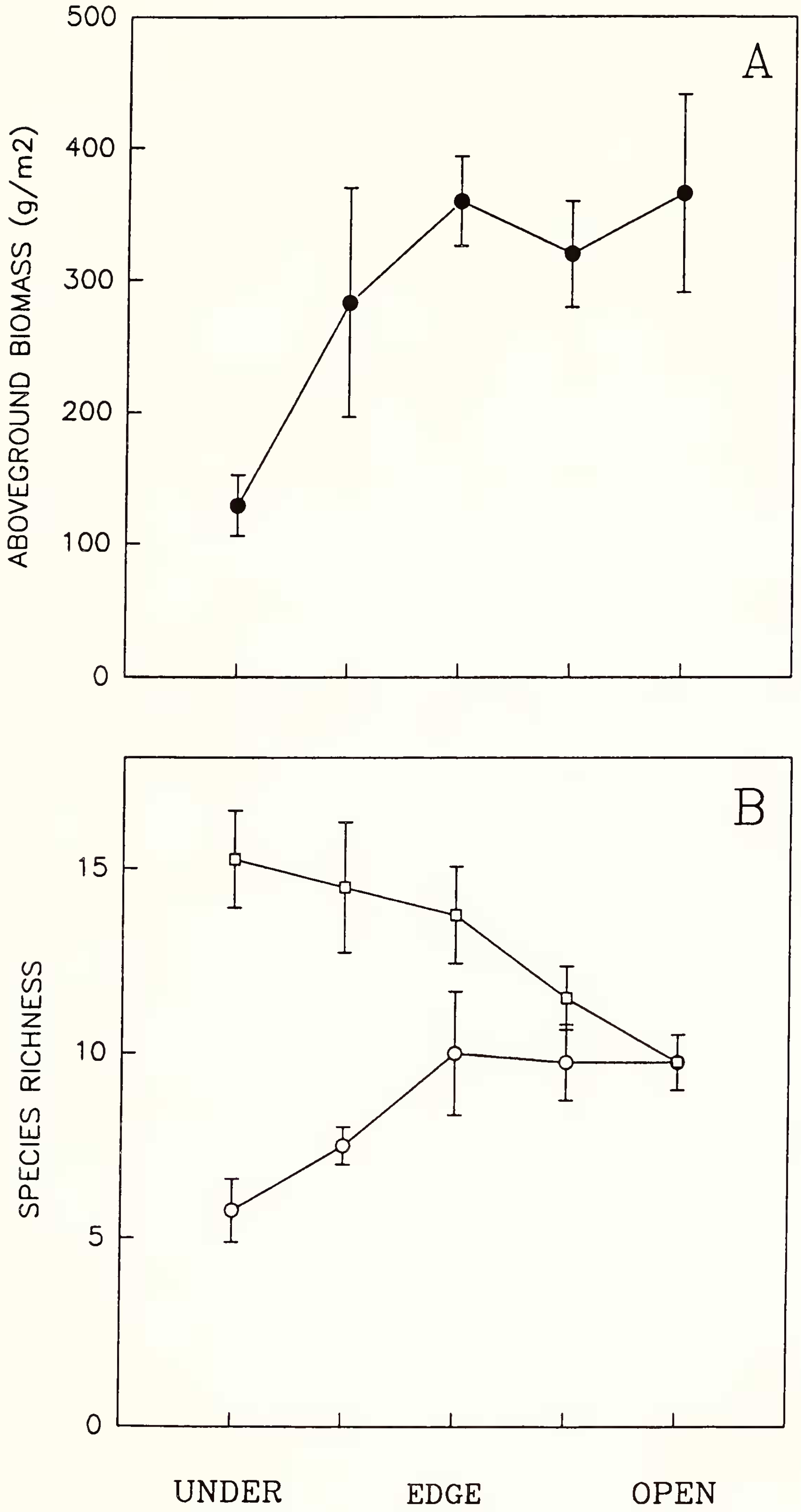

FIG. 3. Aboveground biomass (A), species richness (B, circle) and cumulative species richness (B, square) along the ecotone between the oak understory and open grassland (mean and standard error bar).

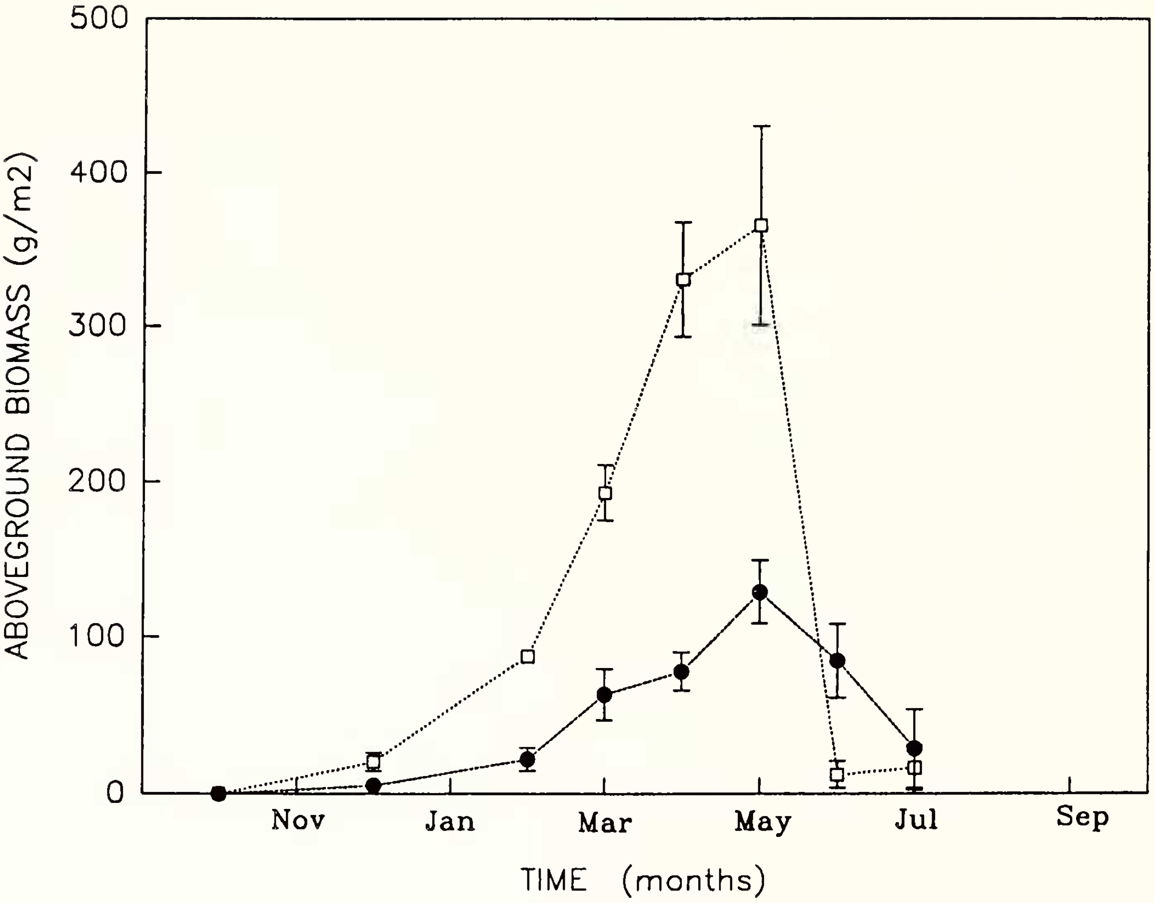

FIG. 4. Monthly aboveground biomass (mean and standard error bar, n = 4) in the oak understory (●) and open grassland (□).

in the open grassland (averages of 7.5–10.0 and 9.8 species 0.0625 m^{-2} respectively) (Fig. 3B). Cumulative species richness along the transect, plotted from the open grassland towards the understory (Fig. 3B), increased up to an average of 15.3 species recorded per transect.

Biomass and diversity. The relationship between aboveground biomass and species richness fitted a second order polynomial regression ($r = 0.49$, $F = 7.47$, $P = 0.009$) (Fig. 6). The calculated maximum for the function (BMD value) was 570.12 g m^{-2}. Oak understory samples showed lower aboveground biomass and species richness than oak canopy edge and open grassland samples.

DISCUSSION

The evergreen oak canopy changes the physical and chemical environment for the herbaceous plants in the understory. Three main factors affecting plant distribution and abundance are light, soil moisture and nitrogen availability. The sharp reduction of light incidence (2.8% of open conditions) precludes seedling establishment

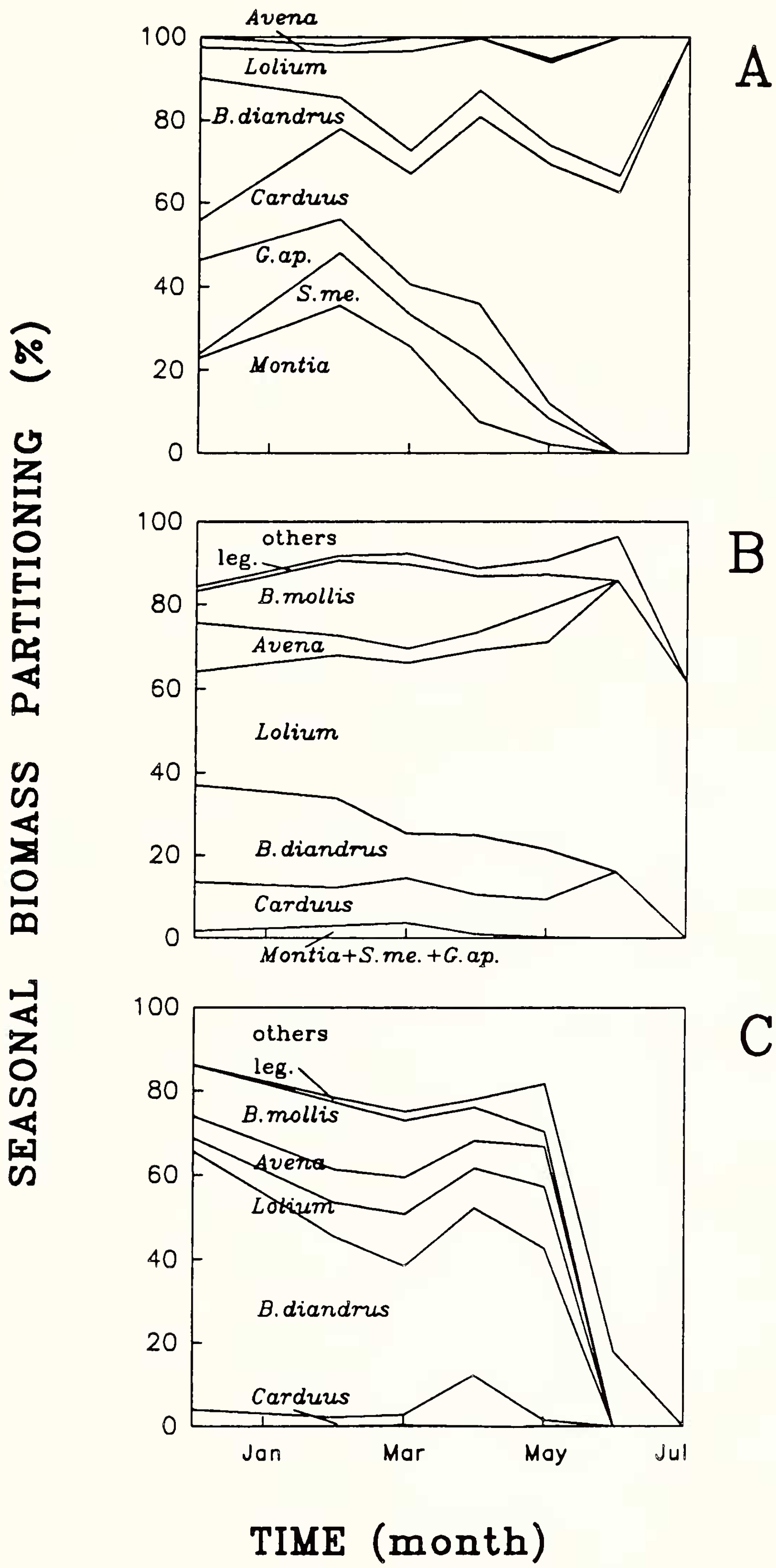

FIG. 5. Percent composition of the seasonal aboveground biomass in the oak understory (A), canopy edge (B) and open grassland (C). Species are named by genus or species (*Bromus*), except abbreviated G.ap. = *Galium aparine* and S.me. = *Stellaria media*, and leg. = legume species.

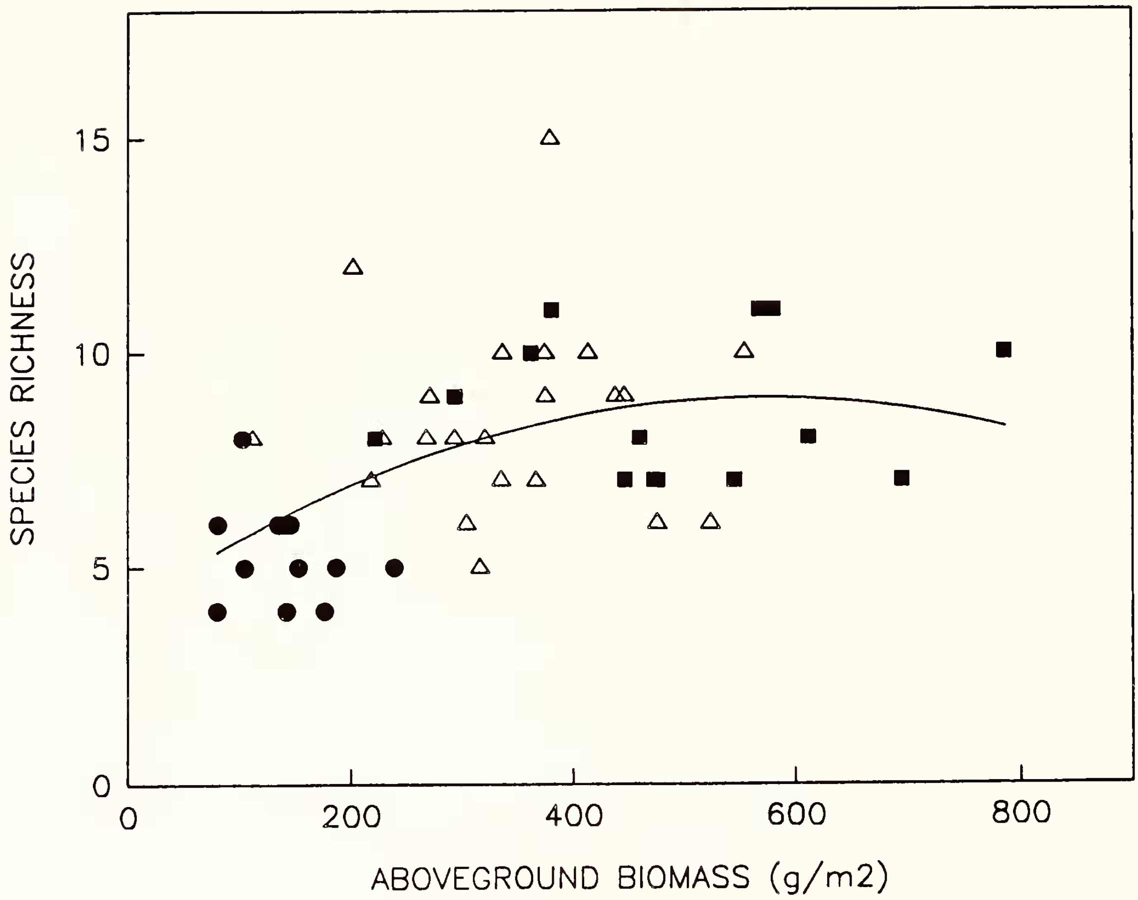

FIG. 6. Relationship between species richness (species number per 0.0625 m^2) and aboveground peak biomass, and fitted second order polynomial regression. Symbols like in Figure 2.

(Marañón and Bartolome 1993) and reduces physiological performance (Parker and Muller 1982) of most grassland species.

Higher soil moisture in the understory during late spring may allow a longer growth persistence, and may favor some perennial herbs like *Elymus triticoides* and *Lathyrus vestitus.* In similar mediterranean-climate Southern Spain, perennial grasses *Dactylis glomerata, Lolium perenne* and *Festuca ampla* were found preferently under oak trees (Marañón 1986), favored by a reduction in the early summer drought stress (Joffre and Rambal 1988).

Higher inorganic nitrogen availability was also found in soils under deciduous *Quercus douglasii* (Jackson et al. 1990), although plant biomass was not affected. Soil ammonium and nitrate concentrations varied seasonally, and during the period of rapid growth (February–April) nitrate pools were almost depleted in the open grassland (Jackson et al. 1990).

Species composition under the oak canopy differs from the adjacent open grassland, as found by several authors in diverse conditions: isolated evergreen *Q. agrifolia* (Parker and Muller 1982), winter deciduous *Q. douglasii* (Holland 1980; McClaran and Bartolome 1989; Callaway et al. 1991; Bartolome and McClaran 1992) and deciduous *Q. garryana* (Saenz and Sawyer 1986). Shade-tolerant species like *Montia perfoliata, Stellaria media* and *Galium aparine* seem to be excluded by competition from the dense open grassland, whereas light-demanding species like *Bromus mollis* and *Hypochoeris glabra* would not survive under closed evergreen oak canopy shade (Marañón and Bartolome 1993). A few species like *Bromus diandrus* and *Carduus pycnocephalus* have a wider ecological range and grow in both contrasted habitats.

Seasonal growth is slower in the understory reaching a lower peak standing crop than in the open grasslands, but the rapid decline in late spring is delayed under the oak canopy. A reduction in herbaceous biomass under evergreen oak was also found by Parker and Muller (1982). However, a variety of responses has been found under deciduous oaks: increasing biomass underneath (Holland 1980), decreasing (McClaran and Bartolome 1989; Bartolome and McClaran 1992) or no significant effect (McClaran and Bartolome 1989; Jackson et al. 1990). Global productivity of the system, oak trees plus herbaceous layer, should be considered for the management of this mosaic landscape (Jackson et al. 1990).

The edge of the oak canopy projection is the ecotone between two contrasted habitats: oak understory and open grassland. In this transition we would expect a higher species density (edge effect, Odum 1971), as found in other similar Mediterranean-climate systems (González-Bernáldez et al. 1969; Marañón 1986). Edge samples, in this study, had a combined species composition, and species density at the ecotone was higher than in the understory but similar to the open grassland. We suggest two reasons influencing the lack of a diversity peak at this ecotone: 1) The total pool of herbaceous species is lower than in the Mediterranean Basin precluding a fine-scale habitat separation. 2) Ungrazed local conditions, in the grassland studied, tend to favor dominant tall grasses and reduce alpha diversity (Heady et al. 1991).

Although the alpha diversity of the herbaceous understory was reduced by the oak canopy effect, the species composition varied compared to the open grassland (beta diversity) resulting in a greater species richness of herbaceous plants for the whole oak woodland-grassland landscape (gamma diversity). From a conservationist viewpoint, oak woodlands are refuges for low competitive, shade-tolerant, native species such as *Montia perfoliata,* in contrast with the open grasslands dominated by Euro-mediterranean colonizers.

At the oak canopy edge, herbaceous plants received a light incidence similar to the open grassland, and ameliorating oak canopy effects on soil moisture and nitrogen content. Peak standing crop is similar to the open grassland but the late spring decline is somewhat delayed. Biomass partitioning tends to be dominated by *Lolium multiflorum* probably benefiting from these peculiar environmental

TABLE 1. VALUES OF BIOMASS FOR MAXIMUM DIVERSITY (BMD) RECORDED BY DIFFERENT AUTHORS FOR HERBACEOUS COMMUNITIES.

Community-type (country)	Biomass for maximum diversity ($g\ m^{-2}$)	Reference
Fens (U.K.)	1500	Wheeler and Giller 1982
Annual grassland (Calif., USA)	570	This study
Herbaceous communities (U.K.)	510	Grime 1979
Wetlands (Netherlands)	400–500	Vermeer and Berendse 1983
Annual grassland (Calif., USA)	350	Bartolome et al. 1980, Heady et al. 1991
Chalk grasslands (Netherlands)	150–350	Willems 1980
Saltmarsh grassland (Spain)	302	García et al. 1993
Grasslands (Spain)	150–300	Puerto et al. 1990
Riverine wetlands (Canada)	300	Day et al. 1988
Lakeshore (Canada)	80–260	Wisheu and Keddy 1989

conditions. In growth experiments, *Lolium multiflorum* was a superior competitor than *Avena fatua* and *Bromus diandrus,* for high nutrient and high temperature treatments (Gulmon 1979).

The same four annual grasses (*Avena fatua, Bromus mollis, B. diandrus* and *Lolium multiflorum*) that dominated open grassland biomass samples, also dominated an ungrazed annual grassland studied in the Berkeley Hills (Ratliff and Heady 1962). Seasonal pattern and partitioning by species was also similar, although *Avena fatua* instead of *Bromus diandrus* was the dominant species. *Lolium multiflorum* had the longest weight persistence during early summer (Ratliff and Heady 1962).

Maximum species richness for an intermediate standing crop is a general trend found in many herbaceous vegetation types, although with different BMD values (Table 1). We found a unimodal relationship between biomass and species richness that supports the model of Grime (1979). The closed shaded habitat is a harsh (sensu Grubb 1987) light-limited environment for most herbaceous species; as a result a few shade-tolerant species form a grassland community of low species richness and low standing crop. In the open grassland, favorable amounts of water and nutrients may also reduce species richness by allowing dominance of tall grasses.

McNaughton (1968) found a negative correlation between species richness and productivity. His data set included highly-productive species-poor grassland on sandstone (similar to our open grassland community) that contrasted to low-productivity species-rich grassland on serpentine. Both light reduction and serpentine nutrient imbalance are harsh conditions reducing standing crop of the grassland community, but the ultimate effects on species diversity seem different. A high diversification of serpentine-tolerant plants is reflected in relatively species-rich communities (Kruckeberg 1984), but comparatively fewer shade-tolerant herbaceous species have evolved in Mediterranean climate, reflected in the species-poor understory communities.

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Literature Cited

Bartolome, J. W., M. C. Stroud, and H. F. Heady. 1980. Influence of natural mulch on forage production on differing California annual range sites. Journal of Range Management 33:4–8.

Bartolome, J. W. and M. P. McClaran. 1992. Composition and production of California oak savanna seasonally grazed by sheep. Journal of Range Management 45:103–107.

Bolsinger, C. L. 1988. The hardwoods of California's timberlands, woodlands, and savannas. USDA Forest Service, General Resource Bulletin PNW-RB-148, Portland, Oregon.

Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. Ecology 72:1484–1499.

Day, R. T., P. A. Keddy, J. McNeil, and T. Carleton. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology 69: 1044–1054.

García, L. V., T. Marañón, A. Moreno, and L. Clemente. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. Journal of Vegetation Science 4:417–424.

González-Bernáldez, F., M. Morey, and F. Velasco. 1969. Influences of *Quercus ilex rotundifolia* on the herb layer at the El Pardo forest (Madrid). Boletin de la Real Sociedad Española de Historia Natural (Biología) 67:265–284.

Griffin, J. R. and W. B. Critchfield. 1972. The distribution of forest trees in California. USDA Forest Service Research Paper PSW 82, Berkeley, CA.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester, U.K.

Grubb, P. J. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. Pp. 99–118 *in* J. H. R. Gee and P. S. Giller (eds.), Organization of communities past and present. Blackwell, Oxford, U.K.

Gulmon, S. L. 1979. Competition and coexistence: three annual grass species. American Midland Naturalist 101:403–416.

Heady, H. F., J. W. Bartolome, M. D. Pitt, M. G. Stroud, and G. D. Savelle. 1991. California grassland. Pp. 313–335 *in* R. T. Coupland (ed.), Ecosystems of the world: natural grasslands, Vol. 8A, Elsevier, Amsterdam, Netherlands.

Holland, V. L. 1980. Effect of blue oak on rangeland forage production in central California. Pp. 314–318 *in* T. R. Plumb (tech. coord.), Ecology, management and utilization of California oaks. USDA Gen. Tech. Report PSW-44.

Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1988. Plant and soil nitrogen dynamics in California annual grassland. Plant and Soil 110:9–17.

———, ———, ———, and ———. 1990. Influence of tree canopies on grassland productivity and nitrogen dynamics in a deciduous oak savanna. Agriculture, Ecosystems, and Environment 32:89–105.

JOFFRE, R. and S. RAMBAL. 1988. Soil water improvement by trees in the rangelands of southern Spain. Oecologia Plantarum 9:405–422.

KRUCKEBERG, A. R. 1984. California serpentines: flora, vegetation, geology, soils, and management problems. University of California Press, Berkeley.

MARAÑÓN, T. 1986. Plant species richness and canopy effect in the savanna-like "dehesa" of S. W. Spain. Ecologia Mediterranea 12:131–141.

——— and J. W. BARTOLOME. 1989. Seed and seedling populations in two contrasted communities: open grassland and oak (*Quercus agrifolia*) understory in California. Oecologia Plantarum 10:147–158.

——— and ———. 1993. Reciprocal transplants of herbaceous communities between *Quercus agrifolia* woodland and adjacent grassland. Journal of Ecology (in press).

MCCLARAN, M. P. and J. W. BARTOLOME. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. Madroño 36:141–153.

MCNAUGHTON, S. J. 1968. Structure and function in California grasslands. Ecology 49:962–972.

MUNZ, P. A. 1968. A California flora and supplement. University of California Press, Berkeley, CA.

ODUM, E. P. 1971. Fundamentals of ecology, 3rd ed. W. B. Saunders, Philadelphia.

PARKER, V. T. and C. H. MULLER. 1982. Vegetational and environment changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. American Midland Naturalist 107:69–81.

PUERTO, A., M. RICO, M. D. MATÍAS, and J. A. GARCÍA. 1990. Variation in structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. Journal of Vegetation Science 1:445–452.

RATLIFF, R. D. and H. F. HEADY. 1962. Seasonal changes in herbage weight in an annual grass community. Journal of Range Management 15:146–149.

SAENZ, L., and J. O. SAWYER, JR. 1986. Grasslands as compared to adjacent *Quercus garryana* woodland understories exposed to different grazing regimes. Madroño 33:40–46.

TER BRAAK, C. J. F. 1988. CANOCO: a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal component analysis, and redundancy analysis (version 2.1). GLW Technical Report: LWA-88-02. Wageningen, Netherlands.

VERMEER, J. G. and F. BERENDSE. 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53:121–126.

WHEELER, B. D. and K. E. GILLER. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above-ground plant material. Journal of Ecology 70:179–200.

WILLEMS, J. H. 1980. Observations on north-west European limestone grassland communities: an experimental approach to the study of the species diversity and above-ground biomass in chalk grassland. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C 83:279–306.

WISHEU, I. C. and P. A. Keddy. 1989. Species richness-standing crop relationships along four lakeshore gradients: constraints on the general model. Canadian Journal of Botany 67:1609–1617.

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